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Ecosystem engineering by large grazers enhances carbon stocks in a tidal salt marsh

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ABSTRACT: Grazers can have a large impact on ecosystem processes and are known to change vegetation composition. However, knowledge of how the long-term presence of grazers affects soil carbon sequestration is limited. In this study, we estimated total accumulated organic carbon in soils of a back-barrier salt marsh and determined how this is affected by long-term grazing by both small and large grazers in relation to age of the ecosystem. In young marshes, where small grazers predominate, hare and geese have a limited effect on total accumulated organic carbon. In older, mature marshes, where large grazers predominate, cattle substantially enhanced carbon content in the marsh soil. We ascribe this to a shift in biomass distribution in the local vegetation towards the roots in combination with trampling effects on the soil chemistry. These large grazers thus act as ecosystem engineers: their known effect on soil compaction (based on a previous study) enhances anoxic conditions in the marsh soil, thereby reducing the oxygen available for organic carbon decomposition by the local microbial community. This study showed that the indirect effects of grazing can significantly enhance soil carbon storage through changing soil abiotic conditions. This process should be taken into account when estimating the role of ecosystems in reducing carbon dioxide concentration in the atmosphere. Ultimately, we propose a testable conceptual framework that includes 3 pathways by which grazers can alter carbon storage: (1) through above-ground biomass removal, (2) through alteration of biomass distribution towards the roots and/or (3) by changing soil abiotic conditions that affect decomposition.

KEY WORDS: Carbon sequestration · Climate change · Coastal wetland · Grazing · Redox potential · Soil compaction · Succession

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INTRODUCTION

The rapid increase in atmospheric carbon dioxide (CO₂) concentration may to some extent be counteracted by carbon sequestration in natural ecosystems (Cannell et al. 1999, Janzen 2004, Le Quéré et al. 2009). Wetlands, including coastal marshes, can play an important role as carbon sinks because of the close feedbacks between vegetation, sedimentation and anoxic conditions, promoting carbon storage (Valery et al. 2004, Duarte et al. 2005, Olsen et al.

2011, Kirwan & Mudd 2012). Once present in the soil, organic carbon can remain buried for a very long time (Connor et al. 2001, Chmura et al. 2003, Duarte et al. 2005, Mcleod et al. 2011). Several studies show that coastal ecosystems, such as tidal marshes, can accumulate a large amount of carbon (Chmura et al. 2003, Duarte et al. 2005, Laffoley & Grimsditch 2009, Mcleod et al. 2011). So far, studies assessing the role of marshes as carbon sinks have mainly focused on abiotic drivers, including sedimentation rate and global warming (Connor et al. 2001, Kirwan & Mudd

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2012, Saintilan et al. 2013, Lovelock et al. 2014), whereas biotic drivers, such as grazer presence, have received much less attention (with the exceptions of e.g. Morris & Jensen 1998, Yu & Chmura 2009, Olsen et al. 2011).

Marshes are used as feeding grounds by many different grazers, ranging from large populations of migratory birds (e.g. Kerbes et al. 1990, Madsen 1991) to livestock; livestock grazing is used as a nature management tool in many European marshes (e.g. Bakker 1989, Kiehl et al. 1996). Grazers can have a large impact on local carbon sequestration in marshes, but results found so far have been limited and contradictory. For example, in some marshes, they decreased organic carbon accumulation by removing above-ground biomass and thus reducing litter production (Morris & Jensen 1998). In other marshes, they positively affected organic carbon accumulation by increasing below-ground biomass production (Yu & Chmura 2009, Olsen et al. 2011) and/or reducing turnover rates (Olsen et al. 2011). Grazing may even turn a marsh from a carbon sink into a carbon source when burrowing crabs increase bioturbation of the soil and remove biomass through grazing (Taylor & Allanson 1993). These contradictory results suggest that the effects of grazers on organic carbon sequestration can differ between systems and/or grazer type, and further study is required before getting to a general mechanistic understanding.

In the present study, we quantified total accumulated organic carbon during marsh development in a northwestern European back-barrier marsh (Schiermonnikoog) dominated by fine-grained sediment accretion (detailed description in 'Materials and methods'). This back-barrier marsh gives us the unique opportunity to study processes over a long time scale due to gradual expansion of the marsh towards the east, resulting in a natural chronosequence (i.e. from 15 to 120 yr old marshes) going from east to west (Olf et al. 1997). The younger marshes are used by small grazers as feeding grounds, with highest grazing intensity at the approximately 30 yr old marsh (van de Koppel et al. 1996, Elschot et al. 2013). The older, most western marshes are grazed by livestock. Previous studies showed that when marshes become older, palatable plant species become slowly replaced by unpalatable ones (Leendertse et al. 1997, Veeneklaas et al. 2013), and the number of small grazers present within the ecosystem reduces (van der Wal et al. 2000, Bos et al. 2004). At this stage, larger grazers become necessary to set back succession (Bos et al. 2002).

In the younger marshes of Schiermonnikoog, small grazers have been excluded from experimental plots for about 15 yr, whereas in the oldest mature marsh, livestock have been excluded for about 20 yr from part of the marsh. The clear gradients in age and grazing type (i.e. small vs. large grazers) as well as long-term enclosure experiments present in the marsh offer an excellent opportunity to quantify the effects of long-term grazing by both small and large grazers on carbon sequestration. Previous studies showed that grazing will not only reduce above-ground biomass but that grazers can also act as ecosystem engineers by increasing the bulk density of the soil layer through trampling (Elschot et al. 2013, Nolte et al. 2013), thereby promoting anoxic conditions and altering the nitrogen cycle (Schrama et al. 2013). Anoxic conditions in the soil are known to reduce the mineralization rate (Aller 1994, Sun et al. 2002, First & Holibaugh 2010). Thus, in this study, we included not only the effects of grazing on biomass of the local vegetation but also studied their impact on local abiotic conditions due to potential soil compaction. In this study, we tested 2 hypotheses: (1) in young marshes, small grazers reduce carbon stocks by removing above-ground biomass of the local vegetation, and (2) in older, mature marshes, large grazers will increase carbon stocks due to trampling, which is known to enhance bulk density (Elschot et al. 2013) and expected thereby to promote anoxic conditions and reduce carbon decomposition in the soil.

MATERIALS AND METHODS

Study site

This study was carried out on the back-barrier marsh of the island of Schiermonnikoog, The Netherlands, located in the Wadden Sea (Fig. 1, 53° 30' N, 6° 10' E). The western and oldest marshes (185 ha) are grazed by cattle in summer with a stocking rate of approximately 0.5 ind. ha⁻¹ (Bos et al. 2002). The more eastern and younger marshes (1450 ha) have never been grazed by cattle but are very important for small grazers. That is, they are grazed by migratory birds such as barnacle goose *Branta leucopsis* and Brent goose *B. bernicla* during winter and spring and by European brown hares *Lepus europaeus* year-round. The highest grazing intensity of geese and hare is found at marshes of intermediate age (van de Koppel et al. 1996, Elschot et al. 2013), where the density of nutritious, palatable species is highest (Olf et al. 1997). Within our study site, we observed

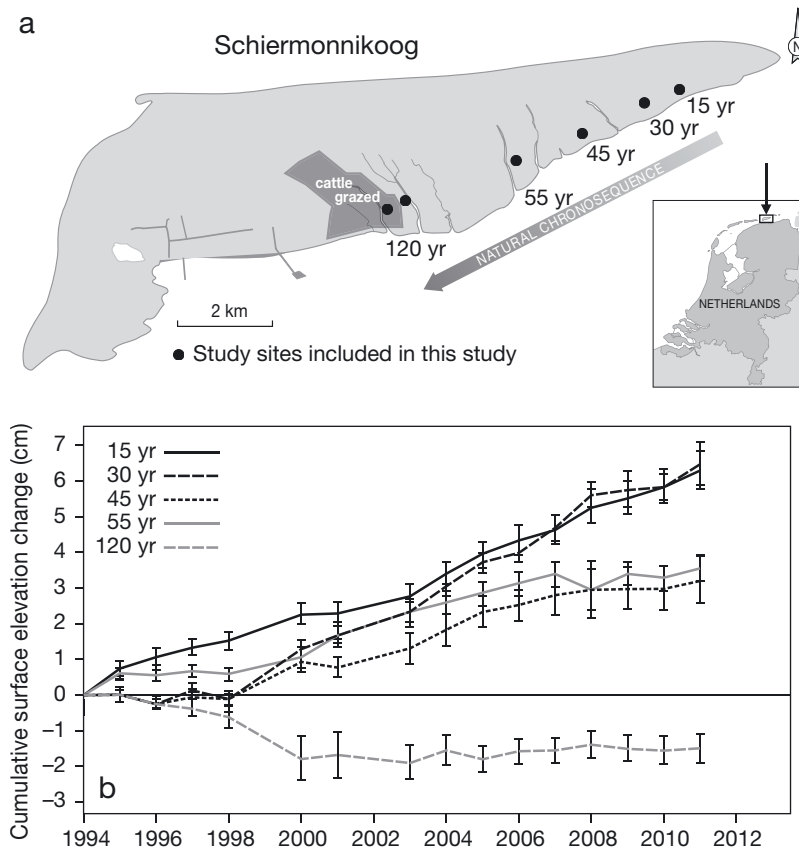


Fig. 1. (a) Back-barrier marsh of Schiermonnikoog, with the natural chronosequence indicated. All sampled locations are indicated by black dots and include approximate ages of each marsh. (b) For each location (indicated by age), the cumulative surface elevation change (cm) between 1994 and 2011 is given. The surface elevation change was not determined in the cattle-grazed marsh

a change in plant composition with increasing marsh age. A vegetation type dominated by *Puccinellia maritima* and *Limonium vulgare* in young marshes is replaced by a vegetation type dominated by *Festuca rubra* and *Artemisia maritima* at marshes of intermediate age (Olf et al. 1997, Bakker et al. 2005). Ultimately, a monoculture of *Elytrigia atherica* becomes dominant in mature marshes (Veeneklaas et al. 2013, Wanner et al. 2014). Large grazers reduce the cover of *E. atherica* and the cover of younger successional species, such as *F. rubra* and *P. maritima*, then increases again (Bos et al. 2002). To quantify the impact of grazing on marsh development, a series of grazing exclosures were placed along the age gradient of the marshes in 1994 (details in next section).

Experimental set-up

Along the chronosequence, 5 locations were selected which differed in age and productivity (Olf et

al. 1997, Kuijper & Bakker 2005). The age of each location (i.e. the age since the marsh was formed by plant colonization on an initially bare tidal flat) was determined using time series of aerial photographs (Olf et al. 1997). This led to approximate marsh age estimates of 15, 30, 45, 55 and 120 yr in 2010, when we took most of our measurements (Fig. 1a, further details are given by Olf et al. 1997). Within the 4 youngest marsh ages, 7 × 7 m grazing exclosures for small grazers were set up in 1994 which excluded grazing by both hares and geese (further details are given by Kuijper & Bakker 2005). Four exclosures in total (1 exclosure per marsh age) were sampled to test the effects of small grazers. The oldest and fifth location, the 120 yr old marsh, was grazed by cattle until 1958, abandoned between 1958 and 1988 and only partly grazed again afterwards. In this study, we measured on the opposite sides of a cattle-grazed fence to estimate the effects of large grazers. Each measurement was taken at a distance of at least 2 m from the fence with 2 m distance between 2 measurement points. Our set-up thus provided

sampling of marshes of different ages and grazing types, albeit in an unbalanced way: about 15 yr with and without small grazers on 15, 30, 45 and 55 yr old marshes vs. about 20 yr with and without large grazers on the 120 yr old marsh.

Net surface elevation change

Rates of surface elevation change (cm) were quantified by annual measurements using duplicate sedimentation–erosion bars (SEBs) (Boumans & Day 1993). The SEBs were established in 1994 on each of the locations, outside the exclosures. We did not include the cattle-grazed area. Cattle are attracted by the poles and affect measurements. Each SEB consisted of 3 poles, which were positioned in a triangular shape with a distance of approximately 2 m between 2 poles. Each pole was embedded at least 1 m in the underlying sandy substrate to ensure stability over time. An aluminum bar perforated by 17

holes placed 10 cm apart could be placed on top of 2 adjacent SEB poles. A small pin placed through each of the holes allowed estimation of the soil surface elevation to the nearest 0.1 cm. Per SEB triangle, this resulted in $17 \times 3 = 51$ measurements, which were averaged to obtain the annual surface elevation change for a given SEB location per year between 1994 and 2011.

Soil sampling and lab analyses

Back-barrier marsh development starts on an initial coarse-grained (sandy) substrate: the base elevation (Olff et al. 1997). Once pioneer vegetation establishes, fine-grained sediment (silt) containing organic carbon accumulates over time on top of the coarse-grained substrate. The sharp border between both sediment types allowed us to exactly sample the total accumulated carbon that has been buried in the fine-grained sediment layer since the marsh was formed. At all 5 marsh ages, fine-grained sediment samples were taken inside and outside the grazing enclosure in June 2010. All measurements inside the enclosures were at least 1 m from the fence to prevent edge effects. Plots outside the enclosure were set up at least 10 m away from the enclosure at a similar base elevation as the underlying coarse-grained substrate. Having a similar base elevation enables us to identify potential effects of grazing on the thickness of the accreted fine-grained sediment layer, as the underlying coarse-grained substrate is not affected by grazing of the marsh.

Per marsh age, we sampled 10 cores from the entire fine-grained sediment layer present on top of the coarse-grained substrate, 5 cores inside and 5 cores outside the enclosure. The cores were taken throughout the entire enclosure to reduce the chances of any pseudo-replication effect. Total core length was compared with the depth of the hole left in the soil surface to exclude samples that were compacted during sampling. We used a Tullgren soil core (10 cm in diameter and 20 cm in length), which is often used for soil fauna sampling (van Straalen & Rijninks 1982, Schrama et al. 2012), allowing us to sample with minimal compaction. If compaction was more than 0.5 cm, the core was discarded, and a new one was taken. From each core, 2 slices of 5 cm were sampled, with the top layer ranging from 0.5 to 5.5 cm and the deeper layer ranging from 5.5 to 10.5 cm depth. We included a top and a deeper layer, as we expected to find the largest impact by the grazers in the top

soil layer. Only the top layer of sediment has been accreted since the enclosures were placed in 1994, considering an average accretion rate of 3 mm yr^{-1} (van Wijnen & Bakker 1997). Additionally, carbon content can change with soil depth (see e.g. Jobbágy & Jackson 2000). Only the top layer could be sampled at the youngest marsh age (15 yr) due to a limited fine-grained sediment layer thickness of approximately 7 cm, but we could sample 2 layers at all other marsh ages. There was a distinct difference between the litter layer and the top of the soil layer. The top 0.5 cm of each core was discarded to avoid the highest root density of the vegetation. To avoid contamination of the fine-grained sediment with coarser sediment, the bottom few centimeters near the underlying coarse-grained substrate were not used for analyses either. Additionally, locally occurring thin coarse-grained layers (generally a few millimeters thick) within the fine-grained sediment layer (de Groot et al. 2011) were avoided. Although these layers might contain carbon as well, the number and thickness of the layers are highly variable and differ between marsh sites (de Groot et al. 2011). The coarse-grained material could increase the bulk density, resulting in a biased organic carbon content found depending on number and sizes of local coarse-grained layers. Additionally, we measured the total fine-grained sediment layer thickness with a smaller corer (diameter 1.5 cm) 4 times in an area of 1 m^2 surrounding each sampled core. This led to average fine-grained sediment layer thicknesses of 7.0 ± 0.4 , 10.1 ± 0.5 , 14.2 ± 0.3 , 13.0 ± 0.5 , 12.0 ± 0.3 and 11.0 ± 0.2 cm at 15, 30, 45, 55 and 120 yr old marshes and at the cattle-grazed marsh, respectively (see also Elschot et al. 2013).

From each slice (of 5 cm thickness), 4 small sub-cores of known volume (diameter 2.1 cm, volume $16.7 \pm 1.9 \text{ cm}^3$) were sampled and freeze dried. After freeze drying, dry bulk density (g cm^{-3}) was estimated by weighing all 4 sub-cores and dividing the weight by their volume. Next, one randomly chosen sub-core was used for organic carbon analysis. All large living root fragments were removed using a 1 mm sieve. From the sieved material, we estimated percentage organic carbon. First, inorganic carbon was removed by *in situ* acidification with ultra-pure hydrochloric acid. Second, samples were combusted at a very high temperature (1010°C) with excess oxygen to make sure all carbon present was turned into CO_2 , which in turn was detected with a thermal conductivity detector (further details are given by Nieuwenhuize et al. 1994).

Soil redox potential and plant biomass distribution

In November 2012, we measured the effects of grazing by small and large grazers on soil redox potential (mV) and plant biomass (g cm^{-2}). Due to practical constraints, we included only 2 sites: (1) the 30 yr old marsh, where the intensity of small grazers is highest (van de Koppel et al. 1996, Elschot et al. 2013), and (2) the mature 120 yr old marsh, where the large grazers were excluded. We measured redox potential at 5 cm depth using 5 platinum electrodes and 1 mercury(I) chloride reference electrode (replicated 15 times). All values estimated with the mercury(I) chloride electrode were converted with the formula $y = 1.675x + 23.79$ mV, which is based on calibration in the lab using a standard hydrogen electrode. Redox potential is used as a proximal measure of soil oxygen content that is potentially available for the decomposition of soil organic carbon (for further information, see van Bochove et al. 2002).

To quantify plant biomass of the local vegetation, we collected small cores (5 cm in diameter and 5 cm in length) inside and outside each enclosure (replicated 10 times). We carefully positioned the cores on the marsh platform to sample both above-ground and below-ground biomass. In the lab, all above-ground biomass was cut from the cores and sorted into dead (litter) and living plant material. The below-ground material was washed over a 1 mm sieve to remove all sediment. Dead organic material present in the soil that could be identified by eye was removed from the samples. All samples were dried at 70°C and then weighed. Additionally, based on the biomass of the living roots and shoots, we calculated the root:shoot ratios (defined as the below-ground living root biomass divided by the above-ground living shoot biomass; Mokany et al. 2006).

Data analyses

Based on the weight percentage of organic carbon together with the sediment bulk density (g cm^{-3}), we quantified organic carbon content (g cm^{-3}) in both the upper and lower fine-grained sediment layer separately. Then, we assigned the carbon content estimated in the top layer to the top 5 cm and assigned the carbon content of the deeper layer to the rest of the fine-grained layer. Thus, if we measured a total fine-grained sediment layer of 14 cm at a specific site, we used 5 cm for the top layer and 9 cm for the

bottom layer. By adding both calculated values together, we estimated total accumulated organic carbon per unit of marsh surface area (g cm^{-2}). This gave us an approximate value for the total organic carbon present in the soil per soil core.

To test the effects of grazing on carbon sequestration, we used 2-way ANOVAs for the small grazers and *t*-tests for the large grazers. Total carbon accumulated, percentage carbon and carbon content per layer were all analyzed separately. Due to the unbalanced design in this study, we had to analyze the small and large grazer effects separately. For the small grazers, both grazing and marsh age were used as predictor variables. If we found a significant interaction effect between grazing and marsh age, we used a Tukey's HSD test to determine whether grazing had a significant effect per marsh age individually. We used linear regressions to determine whether total organic carbon, percentage carbon or carbon content significantly changed with increasing marsh age. To analyze the effects of grazing on biomass distribution and redox potential, we used 2-way ANOVAs, with grazing and site as predictor variables. These were followed by Tukey's HSD tests. Root biomass and root:shoot ratios were log transformed to account for non-normality. *p*-values ≤ 0.05 were considered significant in all analyses. All data were analyzed using R, version 2.13.0 (R Development Core Team 2011).

RESULTS

Net surface elevation change

Average surface elevation change decreased with marsh age (Fig. 1b). Based on the SEBs, we found that the youngest marshes, 15 and 30 yr old, both increased in surface elevation relatively fast, approximately 6 cm in 17 yr. This equates to an average increase of $0.37 \pm 0.01 \text{ cm yr}^{-1}$ for the 15 yr old marsh and $0.38 \pm 0.01 \text{ cm yr}^{-1}$ for the 30 yr old marsh (total surface elevation change divided by the number of years measured). Intermediate-aged marshes, 45 and 55 yr old, had a cumulative surface elevation change of approximately 3 cm. This was an increase of $0.19 \pm 0.01 \text{ cm yr}^{-1}$ for the 45 yr old marsh and $0.21 \pm 0.01 \text{ cm yr}^{-1}$ for the 55 yr old marsh. The oldest location, 120 yr old, showed a negative surface elevation change and decreased 1 to 2 cm between 1994 and 2000. The elevation remained relatively stable between 2000 and 2011 (Fig. 1b).

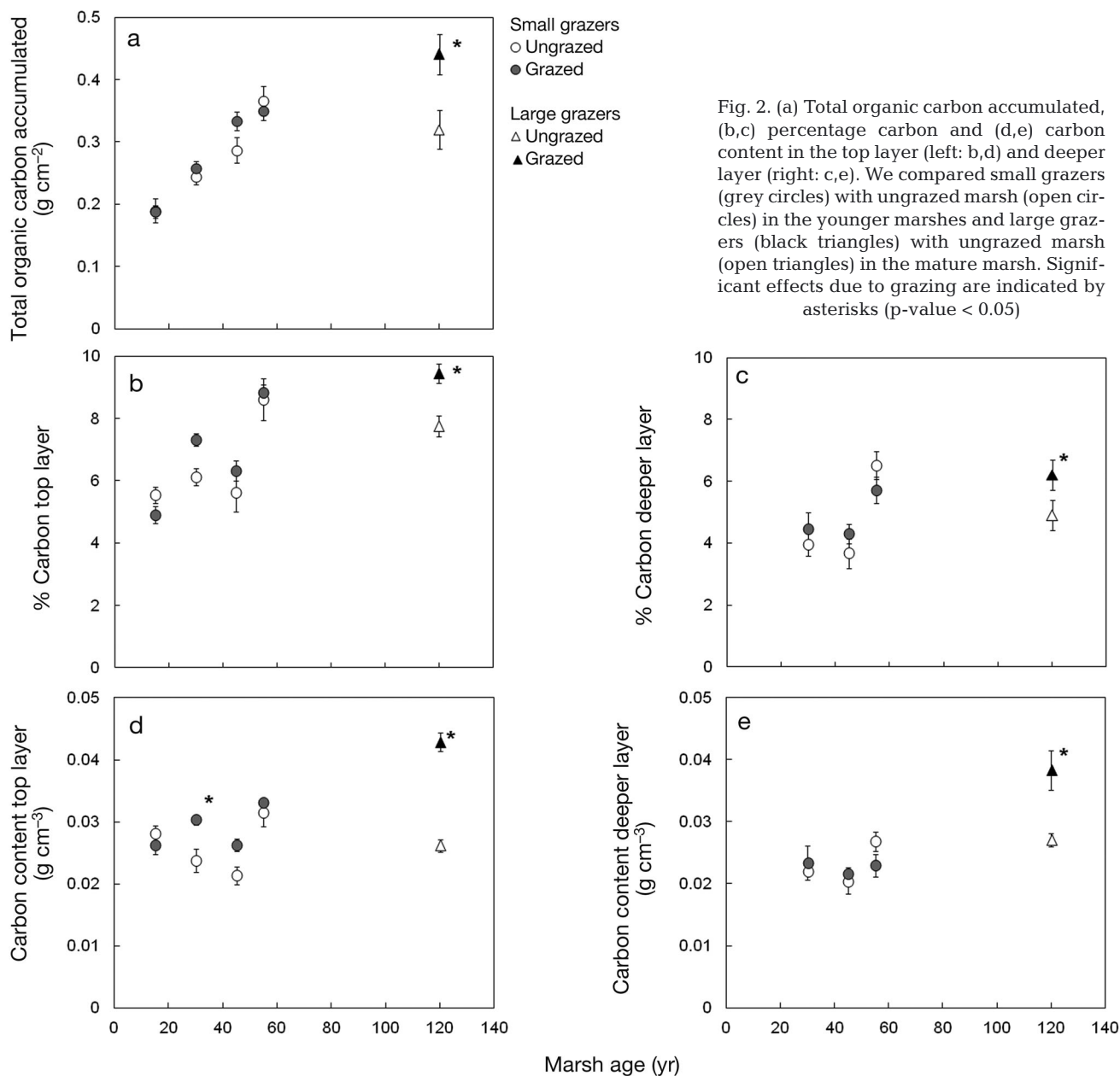


Fig. 2. (a) Total organic carbon accumulated, (b,c) percentage carbon and (d,e) carbon content in the top layer (left: b,d) and deeper layer (right: c,e). We compared small grazers (grey circles) with ungrazed marsh (open circles) in the younger marshes and large grazers (black triangles) with ungrazed marsh (open triangles) in the mature marsh. Significant effects due to grazing are indicated by asterisks (p-value < 0.05)

Effects of age on organic carbon sequestration

Total organic carbon (g cm^{-2} , organic carbon accumulated per unit soil surface) increased significantly with marsh age ($t_{38} = 11.1$, adjusted $R^2 = 0.76$, $p < 0.001$, Fig. 2a). However, the carbon accumulation stabilized at about 0.33 g cm^{-2} once the marsh was approximately 45 yr old (Fig. 2a). The carbon accretion rate was highest at the youngest marsh, approximately $12.6 \pm 0.9 \times 10^{-3} \text{ g cm}^{-2} \text{ yr}^{-1}$ at the 15 yr old marsh (total accumulated carbon divided by marsh age). This sequestration rate decreased rapidly with marsh age (Fig. 2a), ranging from $8.3 \pm$

$0.4 \times 10^{-3} \text{ g cm}^{-2} \text{ yr}^{-1}$ at the 30 yr old marsh, $6.9 \pm 0.4 \times 10^{-3} \text{ g cm}^{-2} \text{ yr}^{-1}$ at the 45 yr old marsh and $6.5 \pm 0.3 \times 10^{-3} \text{ g cm}^{-2} \text{ yr}^{-1}$ at the 55 yr old marsh down to $2.7 \pm 0.1 \times 10^{-3} \text{ g cm}^{-2} \text{ yr}^{-1}$ at the 120 yr old marsh. The percentage carbon increased significantly with marsh age in both the top layer ($t_{38} = 5.4$, adjusted $R^2 = 0.42$, $p < 0.001$) and the deeper layer ($t_{28} = 3.4$, adjusted $R^2 = 0.26$, $p < 0.01$) (Fig. 2b,c). In contrast, organic carbon content per soil volume (g cm^{-3}) was not linearly related to marsh age in both the top layer ($t_{38} = 1.5$, adjusted $R^2 = 0.03$, $p = 0.14$) and the deeper layer ($t_{28} = 1.0$, adjusted $R^2 = 0.0$, $p = 0.34$) (Fig. 2d,e).

Table 1. Effects of grazing on carbon sequestration. The effects of small grazers were tested with ANOVAs, and the effects of large grazers were tested with 2-sample *t*-tests. The models were simplified when interaction effects were not significant. p-values < 0.05 were considered significant and are indicated in **bold**. ns: not significant

	Age			Small grazers			Age × Grazing			Large grazers		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>t</i>	<i>p</i>
Total organic carbon accumulated (g cm ⁻²)	3,35	39.5	<0.001	1,35	1.3	0.26			ns	8.0	6.05	<0.001
% Carbon top layer	3,35	26.8	<0.001	1,35	1.6	0.22			ns	7.9	3.62	<0.01
% Carbon deeper layer	2,26	14.3	<0.001	1,26	0.1	0.76			ns	5.5	2.47	<0.05
Carbon content top layer (g cm ⁻³)	3,32	12.7	<0.001	1,32	8.2	<0.01	3,32	3.6	0.02	7.1	9.49	<0.001
Carbon content deeper layer (g cm ⁻³)	2,26	2.5	0.10	1,26	0.1	0.79			ns	5.0	3.36	0.02

Effects of grazing on organic carbon sequestration

The small grazers did not significantly affect total organic carbon accumulated (Fig. 2a) or percentage carbon (Fig. 2b,c); statistics are given in Table 1. The only significant effect by the small grazers was a small increase in organic carbon content at the 30 yr old marsh in the top layer (Fig. 2d). Large grazers increased the total organic carbon accumulated in the soil substantially, increasing it from 0.32 ± 0.01 g cm⁻² in the ungrazed marsh to 0.44 ± 0.01 g cm⁻² in the grazed marsh (Fig. 2a), i.e. adding more than a kilogram of carbon to the soil per square meter at the 120 yr old marsh. The presence of large grazers on the 120 yr old marsh significantly increased percentage carbon (%) and carbon content (g cm⁻³) in both the top and the deeper fine-grained sediment layer (Fig. 2b–e).

ers (Fig. 3a). Additionally, the redox potential was significantly lower in the mature (120 yr old) marsh compared to the younger (30 yr old) marsh site. Small grazers had no effect on the biomass distribution of the local vegetation (Fig. 3b–d), except for a significant reduction in litter (Fig. 3e). Large grazers altered the biomass allocation by reducing above-ground biomass (Fig. 3b), increasing below-ground biomass (Fig. 3c) and reducing litter (Fig. 3e) significantly. The total living biomass was not significantly affected by the presence of either small or large grazers and was not significantly different between both sites (Fig. 3d). The root:shoot ratio was unaffected by the small grazers and was similar between both marsh sites but increased significantly when large grazers were present (Fig. 3f).

DISCUSSION

Redox potential and plant biomass distribution

Both small and large grazers reduced the redox potential significantly (Fig. 3a, Table 2). The significant interaction effect between grazing and age (Table 2) implies that the effect of large grazers is much more substantial than the effect of small graz-

Our results showed that grazers can have a large impact on carbon sequestration in a salt marsh ecosystem. We reject the first hypothesis, that in young marshes, small grazers reduce carbon stocks by removing above-ground biomass of the local vegetation, as we found no effect of small grazers on total carbon stocks. We accept the second hypothesis, that

Table 2. Effects of grazing on biomass distribution and redox potential tested with ANOVAs. The models were simplified when interaction effects were not significant. p-values ≤ 0.05 were considered significant and are indicated in **bold**. ns: not significant

	Grazing			Site			Grazing × Site		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Redox potential (mV)	1,56	129.2	<0.001	1,56	400.3	<0.001	1,56	49.8	<0.001
Below-ground biomass (g cm ⁻³)	1,37	25.7	<0.001	1,37	13.3	<0.001			ns
Above-ground biomass (g cm ⁻³)	1,36	24.0	<0.001	1,36	26.1	<0.001	1,36	3.6	0.06
Litter (g cm ⁻³)	1,37	18.3	<0.001	1,37	4.0	0.05			ns
Total living biomass (g cm ⁻³)	1,37	0.8	0.37	1,37	2.6	0.11			ns
Root:shoot ratio	1,36	80.8	<0.001	1,36	70.1	<0.001	1,36	27.6	<0.001

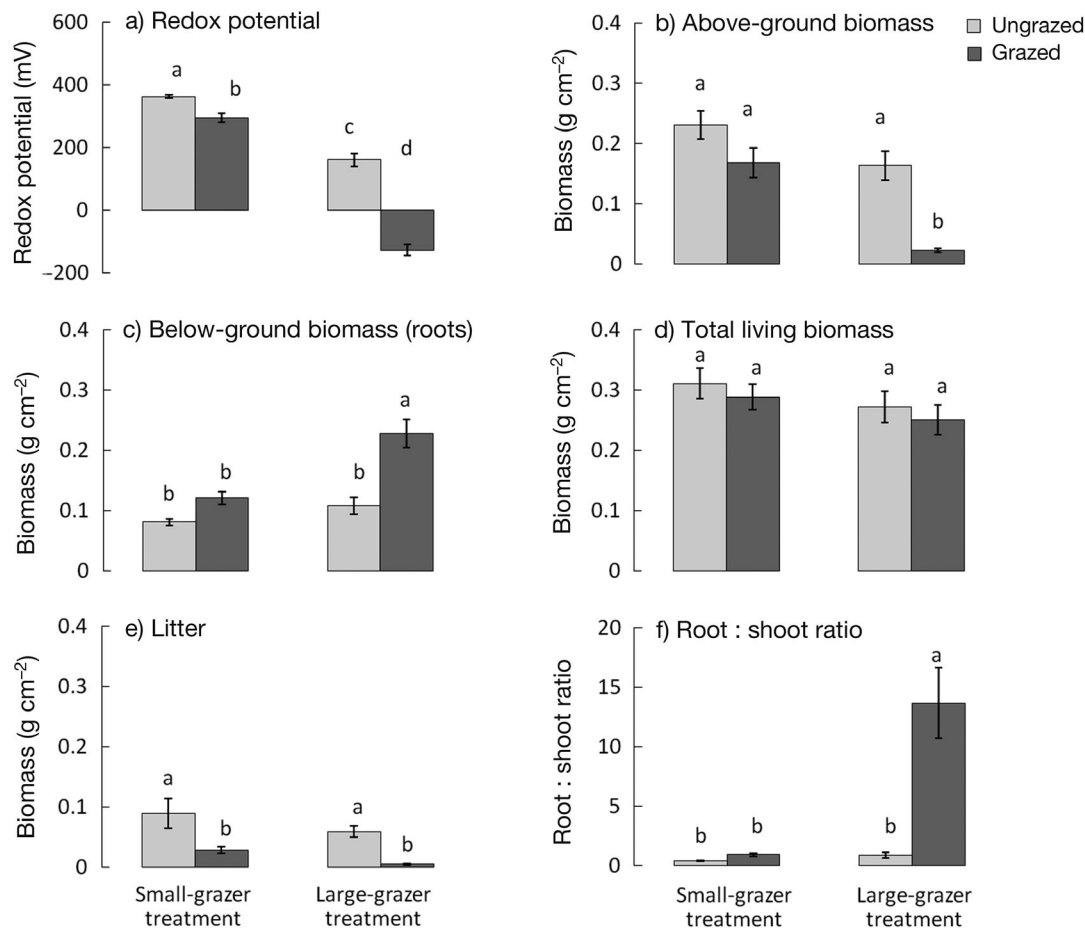


Fig. 3. Differences in (a) redox potential and biomass distribution divided in (b) shoots, (c) roots, (d) total (living) biomass, (e) litter and (f) root:shoot ratios between grazed and ungrazed marsh for small grazers (left) and large grazers (right). Based on Tukey's HSD tests, we assigned different letters when treatments were significantly different (p -value ≤ 0.05)

in older, mature marshes, large grazers increased carbon stocks due to trampling, which has been shown to enhance bulk density (Elschot et al. 2013) and was expected to thereby promote anoxic conditions in the soil, as we found a large increase in carbon stocks and a reduction in redox potential in mature marshes. Previous studies assessing the effect of grazers on carbon sequestration showed that they limit carbon storage by removing above-ground biomass (Morris & Jensen 1998, Sjögersten et al. 2008, Cahoon et al. 2012). However, we found that the indirect effects of grazing (for instance, by altering biomass distribution of the vegetation towards the roots and through compaction of the soil, thereby enhancing anoxic conditions) can outweigh the direct effects of removal of above-ground biomass (Fig. 4). This leads to increased carbon accumulation when large grazers were present. It is generally known that anoxic conditions in the soil will limit mineralization rates by the microbial community

(Aller 1994, Sun et al. 2002, First & Hollibaugh 2010). Therefore, next to above-ground biomass removal and altering biomass distribution in the vegetation towards the roots, we propose that grazers can alter carbon storage via a third important pathway: by compacting the soil, thereby reducing the mineralization rate, enhancing carbon storage and thus acting as an ecosystem engineer (Fig. 4).

Effects of large grazers on soil carbon stocks

This study showed that large grazers had a strong positive effect on carbon accumulation. So far, contradicting results have been reported for the effect of large grazers on carbon sequestration in coastal marshes (Taylor & Allanson 1993, Morris & Jensen 1998, Yu & Chmura 2009, Olsen et al. 2011). An empirical study in 2009 based on sheep grazing showed a local increase in both bulk density and

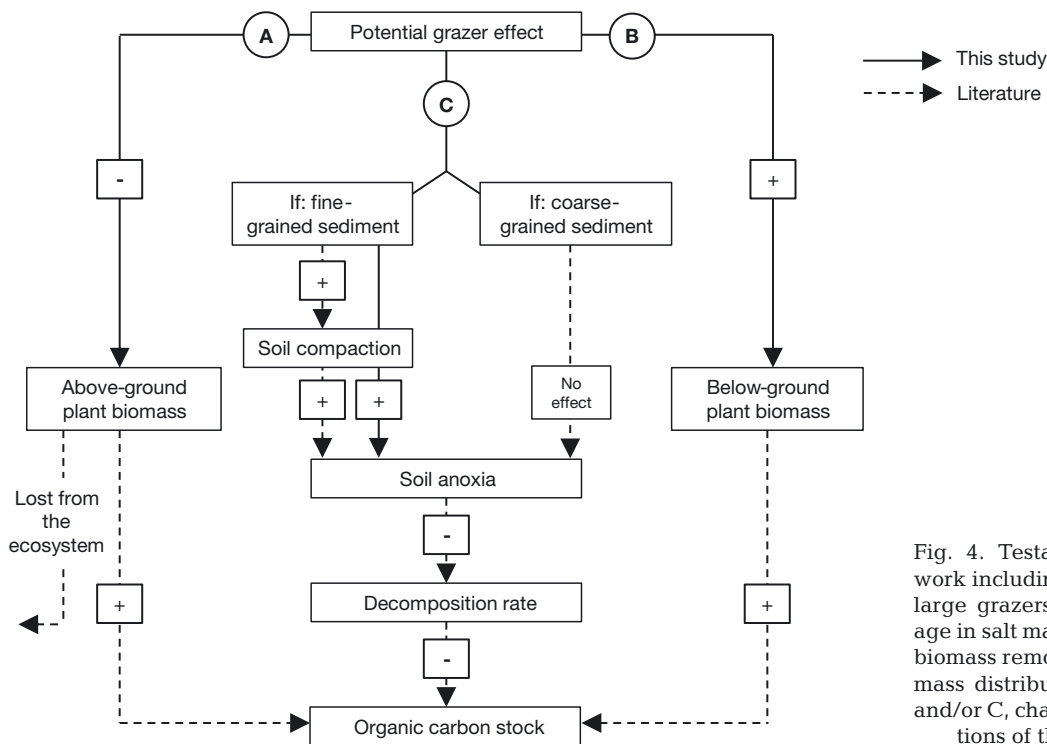


Fig. 4. Testable conceptual framework including 3 pathways by which large grazers can alter carbon storage in salt marshes: A, above-ground biomass removal; B, alteration of biomass distribution towards the roots; and/or C, changing the abiotic conditions of the soil by trampling

organic carbon (Yu & Chmura 2009). This is in line with the results found in the present study. In contrast, cattle grazing on Danish marshes negatively affected organic carbon content (Morris & Jensen 1998), which was attributed to a direct result of above-ground biomass removal by large grazers. The results of our study reveal that large grazers can have an important positive effect on carbon accumulation in marshes.

When negative direct effects by above-ground biomass removal are less substantial than positive indirect effects caused by (1) altered plant biomass distribution towards below-ground root biomass (Zimmerman et al. 1996, Knapp et al. 2008, Cahoon et al. 2012) and (2) changing local soil conditions that reduce carbon decomposition, grazers will enhance carbon sequestration in ecosystems. We propose that soil texture is an important determinant for which effect grazers have within an ecosystem (Fig. 4). Compaction of the soil and subsequent changing soil abiotic conditions will be more substantial in ecosystems with fine-grained (clay and silt) and/or organic-rich (peat) soils and are less likely to occur in ecosystems with more coarse-grained, sandy soils (Fig. 4, Schrama et al. 2013). Ecosystem engineers are defined as 'organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or

abiotic materials' (Jones et al. 1994). Therefore, we can conclude that large grazers can act as ecosystem engineers in ecosystems with fine-grained soils through trampling, thereby compacting the soil and altering carbon decomposition.

Above-ground biomass and litter were lower, but below-ground biomass was higher when large grazers were present (Fig. 3b,c). That grazing-tolerant species invest more energy in their root system compared to above-ground plant parts has been shown in other ecosystems as well (McNaughton et al. 1998, Yu & Chmura 2009, Olsen et al. 2011, Sjögersten et al. 2012). In coastal marshes, below-ground biomass is likely more important as an organic carbon source than above-ground biomass or litter. Most above-ground material will be easily exported as litter towards coastal waters during high tides and storms (Boschker et al. 1999). Additionally, a large part of the organic carbon input is supplied by the inundating water (Boschker et al. 1999) that contains suspended organic matter from non-local macrophytes, benthic microalgae and phytoplankton (Middelburg & Nieuwenhuize 1998). Ultimately, we conclude that grazing increased organic carbon input by increased below-ground biomass production and by reduced decomposition as a consequence of trampling and soil compaction and resulting in increased anoxic conditions in the soil (Fig. 4).

Effects of small grazers on soil carbon stocks

In contrast to other studies showing the negative effects of small grazers on carbon stocks (van der Wal et al. 2007, Sjögersten et al. 2012), we found no significant effect, except for a small increase in organic carbon content (g cm^{-3}) in the top layer at the 30 yr old marsh (Fig. 2d). According to van de Koppel et al. (1996) and Elschot et al. (2013), grazing densities of hare and geese were highest at marshes of intermediate age, namely, at the 30 yr old marsh. This could explain why we only found effects by small grazers at this marsh age. Based on an average surface elevation change of 0.38 cm yr^{-1} (Fig. 1b), only the top layer of the soil contains sediment accreted since the exclosures were placed on the marsh. Therefore, the largest effect of grazer presence should be found in the top layer. Bulk densities of the soil (g cm^{-3}) in both the top and the deeper layer were unaffected by the long-term presence of small grazers (Elschot et al. 2013); hence, the small increase in carbon content is not explained by compaction of the soil layer. We found a small significant reduction in redox potential (Fig. 3a) and a non-significant increase in below-ground root biomass (Fig. 3c). Together, they could explain the small increase found in the organic carbon content in the top layer of the fine-grained sediment layer due to the small grazers. Overall, the small increase found was not substantial enough to affect the total carbon stocks quantified in this study.

Effects of age on carbon sequestration

Carbon storage in the marsh soil is strongly related to marsh age (Fig. 2a). At the youngest marshes, both surface elevation change (Fig. 1b) and the increase in per square meter organic carbon accumulation (Fig. 2a) were highest. A large part of the carbon that accumulates in mineral-based marshes is deposited together with the incoming fine-grained sediment (Boschker et al. 1999). In young marshes, the sediment input is highest (van Wijnen & Bakker 2001), and high saline, anoxic conditions will limit organic carbon decomposition (Hemminga et al. 1991, Aller 1994). With increasing marsh age, the marsh platform increases in elevation (van Wijnen & Bakker 2001), resulting in a reduced sediment deposition rate (Allen 2000) and alleviation of the stressful environmental conditions (Bakker et al. 2005, Davy et al. 2011). At the oldest marsh, the marsh platform did not increase in elevation anymore (a negative surface

elevation change is even shown), and organic carbon content per square meter was no longer increasing. The negative surface elevation change found at the 120 yr old marsh is likely the result of auto-compaction, a natural process that occurs in older, mature marshes, especially after long-term periods of drought (Allen 2000, Bartholdy et al. 2010, Cahoon et al. 2011). At the mature marsh, the total carbon stocks no longer increased. Therefore, we can conclude that the organic matter input from the inundating water together with the local vegetation vs. the output through decomposition has stabilized. Introducing large grazers at this point will increase carbon stocks.

Another potential explanation is a change in vegetation composition with marsh age (Olff et al. 1997, Davy et al. 2011). A study by Jobbágy & Jackson (2000) showed that vegetation type can have a large impact on soil organic carbon through different biomass allocation patterns. This could explain the difference in carbon stocks found in this study. However, biomass allocation of the local vegetation was not significantly different between young marsh and mature marsh (Fig. 4). The positive correlation we found between carbon stock and marsh age is most likely due to continuous burial of organic carbon that is deposited on the marsh surface during high tides, together with root material of the local vegetation, and not due a change in vegetation composition.

We found that the carbon sequestration rate ($\text{g cm}^{-2} \text{ yr}^{-1}$) reduces with age of the marsh and that carbon stocks stabilized when marshes reached 45 yr of age. Most studies estimating organic carbon sequestration in coastal wetlands generally do not take age of the ecosystem into account (e.g. Connor et al. 2001, Chmura et al. 2003, Mcleod et al. 2011). In line with our results, a study in riverine floodplains showed that soil organic carbon accumulated rapidly at young successional stages but that sequestration rate reduced with increasing age and stabilized after approximately 100 yr (Zehetner et al. 2009). They found sequestration rates of $180 \text{ g m}^{-2} \text{ yr}^{-1}$ over the first 25 yr and $100 \text{ g m}^{-2} \text{ yr}^{-1}$ over 100 yr. In comparison, we found a rate of $126 \text{ g m}^{-2} \text{ yr}^{-1}$ over 15 yr and $27 \text{ g m}^{-2} \text{ yr}^{-1}$ over 120 yr, which is lower than the average rate of $210 \text{ g m}^{-2} \text{ yr}^{-1}$ as was estimated for salt marshes in general (Chmura et al. 2003). Our accretion rates are lower, which could be explained by the low sedimentation rates found on European back-barrier marshes (van Wijnen & Bakker 1997) compared to mainland marshes (Nolte et al. 2013). Other studies that estimated car-

bon sequestration rates along natural chronosequences in wetlands found that the percentage carbon in the soil increased with age of the ecosystem (Cornell et al. 2007, Osland et al. 2012, Lunstrum & Chen 2014). However, most of these studies had limited chronosequences of approximately 30 yr, and the ecosystems might not have reached a stable state yet (e.g. Craft et al. 2003, Cornell et al. 2007, Osland et al. 2012). Coastal wetlands are now recognized as ecosystems that can store large amounts of carbon (Chmura et al. 2003); therefore, it is important to understand which factors control carbon accumulation in these ecosystems. Further studies that include long-term chronosequences, ranging over centuries, will be necessary to determine whether carbon accumulation changes with age.

Pseudo-replication

This experiment gave us the unique opportunity to study the long-term effects of grazing on carbon sequestration. However, we do need to address the potential problem of pseudo-replication. As only one enclosure per site was sampled, this could result in samples not being completely independent from one another. The enclosures were of a relative large size (7×7 m), however, which allowed us to spatially spread the samples throughout each enclosure to minimize any pseudo-replication effect from samples taken too close together. The effects of large grazers on carbon sequestration and redox potential as well as biomass distribution were so profound that we consider the results to be robust. However, as we only tested the effects of large grazers on one marsh site, this study should be replicated in more marshes to determine whether this is in fact a general mechanism. The minimal effects we found on the 30 yr old marsh by small grazers on carbon content and redox potential as well biomass distribution need further investigation. We consider the effects of small grazers on total carbon accumulated to be robust, as all 4 sites showed the same result: namely, that small grazers had no significant effect on the total carbon accumulated.

Implications for management

Our results imply that because we can manage livestock grazing in many ecosystems, it being a well-used management tool in European marshes

(Dijkema 1990, Esselink et al. 2009), we can manage and enhance carbon stocks in mature marshes and potentially in other terrestrial ecosystems (Sjögersten et al. 2012). However, the balance between indirect and direct effects due to grazers needs to be determined in each individual ecosystem independently. Due to current anthropogenic disturbances, natural grazers—especially the large ones—are reduced in numbers in many ecosystems (e.g. de Visser et al. 2011), and climate change is expected to further increase species loss (Thomas et al. 2004, Bellard et al. 2012). When the direct effects of biomass removal is the predominant grazing effect, increased grazing intensity in well-drained sandy grassland systems such as savannas could decrease carbon sequestration. However, trampling by large grazers will most likely increase local carbon sequestration, and this may be the predominant effect in wetland ecosystems such as marshes with fine-grained soils. Although our results are limited to a single barrier island, the mechanisms are potentially general and justify testing in other ecosystems with different grazer species and soil types (Fig. 4). Improving our understanding of the effect of grazers on carbon sequestration may allow us not only to control but also to enhance the ability of ecosystems to act as carbon sinks.

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